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## SEX DIFFERENCES IN NEST VISITATION BY CHICK-REARING MARBLED MURRELETS

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**Abstract.** We report a significant male bias in dawn and dusk nest visitations of breeding, radio-marked Marbled Murrelets (*Brachyramphus marmoratus*) during the chick rearing period in Desolation Sound, British Columbia, Canada, from 1998–2000. Overall visitation rates of males during chick rearing were 1.3 times greater than those of females. Dusk visitation rates by males with active nests were 1.8 times greater than those of females. Male visitation rates were similar between early and late chick rearing, both within and among individuals. However, female visitation rates during late chick rearing were significantly lower than female rates early in rearing, both within and between individuals. In addition, between-sex comparisons of nest visitation during early and late chick rearing showed significant reductions in female effort relative to males, only during late chick rearing. These results suggest that male birds may provision chicks more often than females, especially during the last half of chick rearing. These findings offer a behavioral explanation for the annual male bias of birds flying inland during the chick rearing period at Theodosia Inlet in Desolation Sound from 1994–1999. Although female-biased provisioning has been documented in several species, male-biased provisioning has not been widely reported in other alcids.

**Key words:** *Brachyramphus marmoratus*, British Columbia, male bias, Marbled Murrelet, provisioning, radio-telemetry, sex ratio.

Diferencias de Sexo en la las Visitas al Nido  
en *Brachyramphus marmoratus*

In this paper we report on relative nest site visits of male and female radio-marked Marbled Murrelets during the chick rearing period in Desolation Sound from

TABLE 1. Male and female Marbled Murrelet nest visitation rates during early and late chick rearing. Visitation rates are mean  $\pm$  SE number of detections per 4-hr observation session. Tests for differences in visitation rates between sexes and among individuals were conducted with all available independent datapoints. Reported sample sizes are subsets of the total number of birds tracked (23 females, 25 males). Unless noted, all tests are one-tailed. Early 5 nestling days 1–15; late 5 nestling days 16–30.

	Female ( <i>n</i> )	Male ( <i>n</i> )	<i>P</i>
Female vs. male <sup>a</sup>			
Early	0.62 $\pm$ 0.05 (16)	0.73 $\pm$ 0.06 (17)	0.09
Late	0.43 $\pm$ 0.05 (16)	0.59 $\pm$ 0.08 (15)	0.05
	Early ( <i>n</i> )	Late ( <i>n</i> )	
Within sex, among individuals			
Female <sup>a</sup>	0.67 $\pm$ 0.08 (7)	0.41 $\pm$ 0.07 (7)	0.02
Male <sup>b,d</sup>	0.83 $\pm$ 0.08 (10)	0.62 $\pm$ 0.09 (8)	0.11
Within individuals <sup>c</sup>			
Female	0.59 $\pm$ 0.06 (9)	0.45 $\pm$ 0.08 (9)	0.04
Male <sup>d</sup>	0.58 $\pm$ 0.07 (7)	0.55 $\pm$ 0.13 (7)	0.87

<sup>a</sup> Two-sample *t*-tests.

<sup>b</sup> Mann-Whitney-Wilcoxon test.

<sup>c</sup> Paired *t*-tests.

<sup>d</sup> Two-tailed test.

inland during chick-rearing relative to morning captures. A significance level of 5% was used for statistical tests. Results are presented as means  $\pm$  SE. All analyses were done with Minitab release 13.1 (2000).

## RESULTS

On average we conducted 11.0  $\pm$  2.0 observation sessions per male and 12.1  $\pm$  1.7 per female per year over three years of study. Thirty-three percent of sample birds were monitored throughout early and late chick rearing, while the remainder were observed only during one-half of their chick-rearing period. The mean total observation period was 11.6 days per bird. Males visited their nests 1.3 times as often as females ( $t_{45} = 2.4$ ,  $P = 0.01$ ). The discrepancy between male and female visitation rates was even greater (1.8 times) during evening visits ( $W = 710.5$ ,  $P = 0.02$ ,  $n = 23$  females, 25 males). Both within and among individuals, male visitation rates did not significantly differ between early and late chick-rearing, while female visitation rates significantly decreased between these two periods (Table 1). In addition, male and female visitation rates did not significantly differ in early chick rearing, but female rates were significantly lower than those of males during late chick rearing (Table 1). All 15 of the nest trees we climbed showed evidence of a nest, including chick feces and down.

We had continuous late-chick-rearing monitoring data on only one of the two nests where both parents were radio-marked. In the final eight days of chick-rearing at this successful nest, the male visited the nest 2.3 times as often as the female ( $n = 23$  total visits by both parents). Eighty-six percent (6 of 7) of the female's visits were AM feedings compared to 63% (10 of 16) for the male.

Although Vanderkist et al. (1999) found no significant difference in male bias between the morning and

evening captures of birds flying inland at Theodosia Inlet, we reanalyzed the capture data with an additional two years of results. Pooling capture data (1994–1999,  $n = 680$ ), male bias in birds flying inland during the likely chick-rearing period was greater in the PM (2.29:1) than in the AM (1.64:1;  $\chi^2_1 = 9.1$ ,  $P = 0.01$ ).

## DISCUSSION

Male Marbled Murrelets were detected visiting or traveling toward active nests during the chick-rearing period significantly more often than females. This trend was greater during trips made at dusk. During the late chick-rearing period, females significantly reduced their rate of nest visitation, both within and between

Sex-biased provisioning in altricial birds takes many forms. Male-biased provisioning is observed in several seabird species, including many larids (Fasola and Saino 1995) and albatrosses (Huin et al. 2000, Weimerskirch et al. 2000). However, this pattern is reversed in most studies of the Alcidae. Creelman and Storey (1991) found female Atlantic Puffins (*Fratercula arctica*) making more chick-provisioning visits than males. A similar trend has been observed in Common Murres (*Uria aalge*; Wanless and Harris 1986) and Crested Auklets (*Aethia cristatella*; I. Jones 1993). However, male puffins and murres are involved in much more territory defense during the breeding season than females (Creelman and Storey 1991, Wanless and Harris 1986). Increased territory defense by males was observed throughout the breeding period, primarily pre-egg-laying in murres and during chick rearing in puffins (Creelman and Storey 1991, Wanless and Harris 1986). Thus, contrasting sex biases are observed in allocation of resources for different aspects of reproductive effort. If male Marbled Murrelets do not invest in territorial behavior to the same extent as male alcids of colonial species, perhaps they have more energetic resources to devote to provisioning.

While our results on overall feeding bias are opposite to findings for most other alcids, a study of Dovekies (*Alle alle*) showed male provisioning bias late in chick-rearing. While female Dovekies provide the majority of chick provisioning until late chick-rearing, they cease provisioning about five days before the chick fledges, after which the male does all feeding (Taylor and Konarzewski 1992).

The overall male bias of inland trips by confirmed breeders reported here (1.3 times) is markedly less than the 1.8 times male bias reported by Vanderkist et al. (1999). Our result may be due to our limited sample of birds of known sex and breeding status. As suggested by Vanderkist et al. (1999), there may also be a male bias in nonbreeding birds flying inland to prospect for breeding sites or defend territories. Our radiotelemetry surveys have focused on breeding birds, but there is a need for future study to quantify the inland behavior of known nonbreeders.

The decrease in female effort during the late chick-rearing period is similar to trends observed in other birds outside the Alcidae, such as Pacific Loons (*Gavia pacifica*; Petersen 1989) and Merlins (*Falco columbarius*; Sodhi 1993). The behavioral change observed in Marbled Murrelets may be due to the likely high cost of egg production in this species. Marbled Murrelet eggs are approximately 20% of adult body mass (Nelson 1997), in addition to the mass increase and energetic cost of ovary development to females for their one-egg clutch. Monaghan et al. (1998) showed that parental effort is mediated through the negative influence of egg production on female condition. Therefore, the decrease in female investment during the chick-rearing period may result from more female self-feeding to recover egg production costs. However, there is little empirical evidence that supports an immediate "egg cost" hypothesis in murrelets. After egg

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